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Sediment Correlates to Density of *Crepidula fornicata* Linnaeus in the Pataguanset River, Connecticut

by

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Abstract. Relationships among the density of *Crepidula fornicata* and various characteristics of the sediments with which it is associated in the Pataguanset River, Connecticut, were examined. The population is located in an area transitional between a relatively deep channel and an intertidal sand flat. Over 90% of the stacks were situated so that most of the snails were in direct contact with a soft, silty substrate. The density of snails ranged from 0 to 43 individuals/m^2 and the greater densities were associated with sediments that had a high percent cover of solid substrate, relatively high silt and clay content, small mean grain diameter, and high organic content. Multiple regression analysis indicates that 67% of the variance in density can be attributed to changes in percent cover of solid substrate and another 19% of the variance in density can be attributed to changes in the organic content. The rest of the independent variables did not significantly correlate with variance in density. The significance of these data in relation to the ecology of *C. fornicata* is discussed.

INTRODUCTION

THE RELATIONSHIP between benthic organisms and various characteristics of the substrates with which they are associated has been of interest to ecologists for a long time (BADER, 1954; THORSON, 1966; SANDERS, 1958, 1960; DRISCOLL & BRANDON, 1973; DRISCOLL, 1967; RHOADS & YOUNG, 1970; CRAIG & JONES, 1966). A basic generalization that has emerged from studies on fauna-sediment relationships is that epifaunal suspension feeders are usually associated with coarser-grained or firm bottoms while deposit feeders are usually associated with finer-grained or soft substrates (DRISCOLL & BRANDON, 1973; DRISCOLL, 1967; RHOADS & YOUNG, 1970; SANDERS, 1958, 1960; CRAIG & JONES, 1966). One apparent exception to this generalization is the association of the epifaunal suspension feeder, the slipper shell *Crepidula fornicata* Linnaeus, 1758, with soft muddy substrates (DRISCOLL, 1967; DRISCOLL & BRANDON, 1973; BARNES *et al.*, 1973).

It has been suggested that this apparent anomaly can be explained by the fact that individuals of *Crepidula fornicata* are found in stacks, raising them far enough above the soft bottom to prevent fouling of their feeding mechanisms by suspended or resuspended sediment (FRETTER & GRAHAM, 1962; DRISCOLL, 1967). However, using scuba, we have observed living populations of this organism in which most of the stacks were lying on their sides buried at least one centimeter in the soft, silt substrate. Because they can live in direct contact with silt substrates, there may be other explanations for this anomaly. This paper examines changes in the density of a *C. fornicata* population in the Pataguanset River, Black Point, Connecticut (Figure 1) along a gradient of sediment types ranging from coarse sand and pebbles at the mouth of the river to soft mud 230 m upstream, in an attempt to elucidate effects of substrate type on the biology of these animals.

MATERIALS AND METHODS

Density of the animals was measured using scuba along 50-m transects by counting all of the animals in consecutive 1-m^2 quadrats. At the same time, the number of snails in each stack and the objects to which the snail at the bottom of each stack was attached were recorded. Bottom water samples were collected using a LaMotte water sampling bottle. The salinity of the water samples was measured with an American Optical, temperature-compensated refractometer and the temperature of the samples was measured using a mercury thermometer. Bottom topography was mapped using a surveyor's level and leveling rod.

A total of 21 transects was examined for the presence of *Crepidula fornicata*. Transect 1 was located on the east side of the mouth of the Pataguanset River and consecutive transects were 20 m apart. Each transect was situated

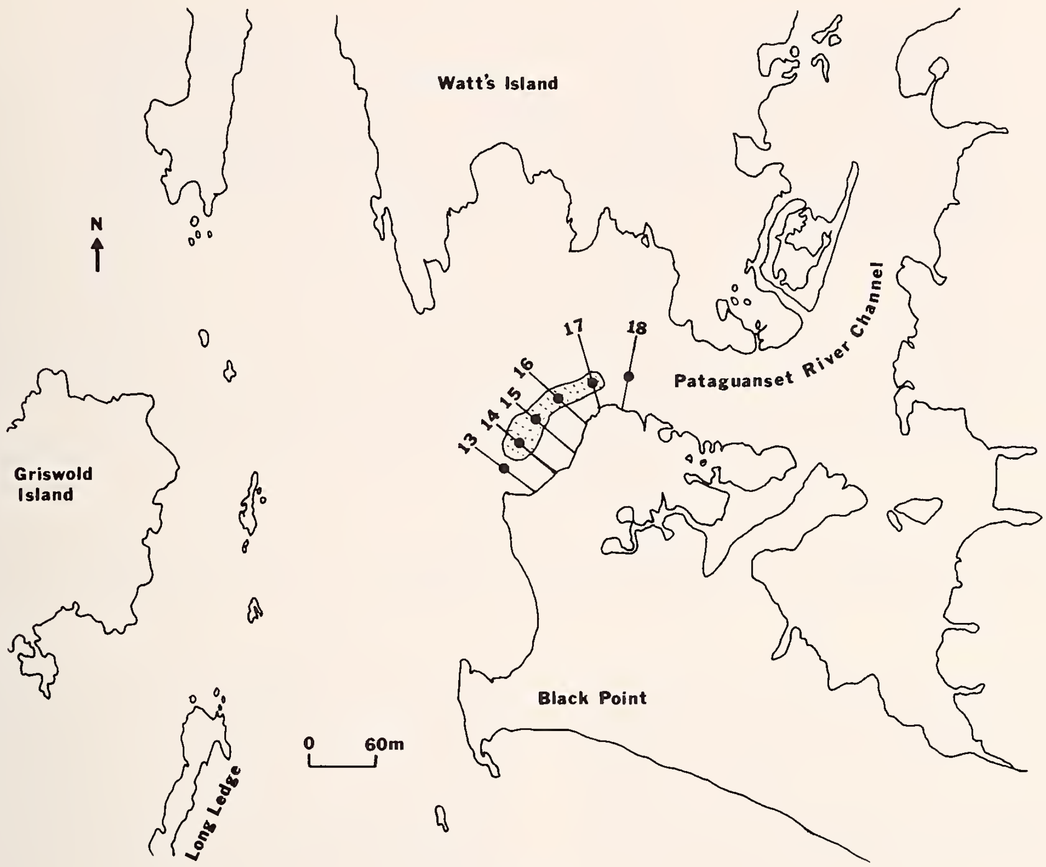

Figure 1

Map of the study area showing the location of transects 13 through 18, the limits of the population of *Crepidula fornicata* (the stippled area), and the location of the sample stations (black dots).

perpendicularly to the shoreline. This examination showed that there was a population of *C. fornicata* associated with transects 14 through 17 (Figure 1). The rest of the transects were either void of *C. fornicata* or contained only one or two stacks. The density of the snails was highest on transect 16 and fell off rapidly either upstream or downstream (Table 1). The highest density for each transect was always found approximately in the center of the population. The quadrat on each transect with the highest density was chosen as a sediment sampling station (Figure 1). Two other stations with no snails were identified on transects 13 and 18 by extrapolating the location of the population to these transects. These stations, therefore, represented areas that had densities ranging from 0 to 43 snails/m^2. Four sediment samples (approximately 200 g each) were collected at each station by scooping the top 2 cm of the sediment into a wide-mouth jar and immediately capping it. The samples were washed in distilled water to remove salt, centrifuged at 12,000 × g for 30 min, and oven dried at 75°C. Two of the samples were separated according to particle size using a series of U.S.A. Standard Testing Sieves and each size class was weighed to the nearest 0.1 g. The silt and clay fraction (particles less than 4.20 ϕ [0.055 mm]) for each sample was suspended in 50 mL of distilled water in a graduated cylinder and particles were separated according to size classes by the pipetting

Table 1

Location of the sediment sampling stations and density of *Crepidula fornicata* at each station.

Transect	Quadrat no.	Density (snails/m^2)
13	25	0
14	33	17
15	42	36
16	38	43
17	17	27
18	19	0

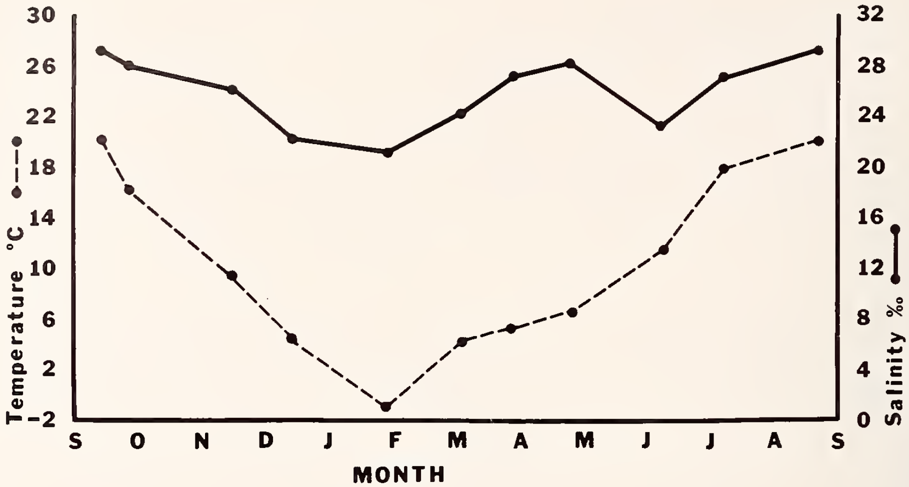

Figure 2

Temperature and salinity of water taken from the station on transect 15 from September 1981 to August 1982.

method of KRUMBEIN & PETTIJOHN (1938). The other two samples were oven dried at 75°C, weighed to the nearest 0.1 mg, combusted at 650°C for 6 h, cooled and reweighed to obtain an estimate of the organic content of the sediment. Percent cover of solid substrate was measured by collecting all of the hard material on the surface of the sediments (including shells, rocks, bottles, and wood) in replicate 0.25-m^2 quadrats at each station. The outline of each piece of material was traced on graph paper, cut out, and weighed to the nearest 0.1 mg on a Mettler Balance. The weights were compared to the weight of a 4-cm^2 piece of graph paper to calculate the surface area covered by each piece.

Observations of the movement of particles into the mantle cavity of *Crepidula fornicata* were made in the following manner. Surface sediments collected from the study site were suspended in seawater, poured into a large glass fingerbowl, and allowed to settle on the bottom of the fingerbowl until the water was clear (usually about 3 h). Stacks of *C. fornicata* were placed on the sediments with either their left or right side down and carefully pushed into the sediments until the lower edge of the shells was about 1 cm below the surface of the sediments, corresponding to the field conditions. Observations were made immediately and at one-hour intervals for 6 h with a dissecting microscope. Initial observations indicated that postural movements of the snails were important for the movement of particles into the mantle cavity. We measured these postural movements in the following way. Stacks containing only two *C. fornicata* individuals were made by fragmenting larger stacks. The animals on the bottom of the small stacks were dissected from their shells, resulting in single individuals attached to empty *C. fornicata* shells. A small hole was drilled in the anterior-most margin of each live snail's shell. The live snails were connected to the displacement transducer of a physiograph by tying one end of a thread to the transducer and the other end to the shell through the hole. The empty *C. fornicata* shells to which the live animals were attached were anchored in a fingerbowl (which functioned as a counterweight) by four plastic coated copper wires with one end embedded in wax. This apparatus was lowered into a battery jar containing aerated seawater and movements of the snail were recorded with the physiograph. Measurements were made in the presence and absence of sediments.

RESULTS

Physical Characteristics at the Study Site

Water temperature (Figure 2) between September 1981 and August 1982 ranged from 22°C (in August) to −1°C (in January). Bottom salinity within the population of *C. fornicata* ranged from 19 to 29‰ (Figure 2) and was never different from surface salinity. These data were taken at high tide and represent maximum values; however, the salinity at low tide was never more than 3‰ less than at high tide.

Bottom profiles (Figure 3) revealed that the *Crepidula fornicata* population was located in an area transitional between a channel 2 m deep and an intertidal sand flat. The tidal range at the study site is about 1 m and all stacks were located below this range. Tidal flow velocity at this site was high although rates were not measured. The percent silt and clay of the sediments in the study area ranged from 0.2% where there were no *C. fornicata* to 19.6% where the density was intermediate. Mean grain diameter ranged from 3.6 ϕ (0.08 mm) in areas of inter-

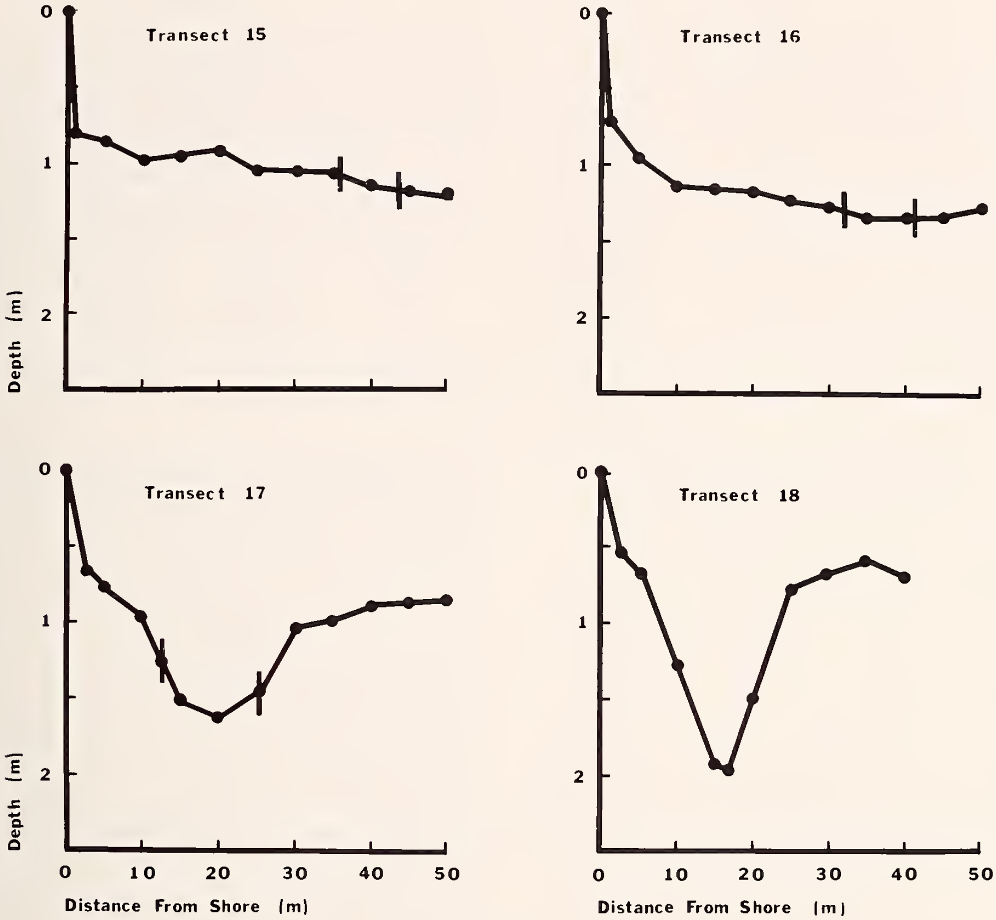

Figure 3

Bottom profile of transects 15 through 18 showing transition between channel and sand flat. Depths were taken from mean high tide. The vertical bars represent the limits of the *Crepidula fornicata* populations (there were no *C. fornicata* found in transect 18).

mediate density of *C. fornicata* to 2.4 ϕ (0.185 mm) in areas without *C. fornicata*. Sediment sorting (as measured by the Trask Sorting Coefficient) became increasingly poor with decreasing grain diameter (Figure 4). The organic content of the sediments ranged from 0.44% to 1.79%. Scattergrams of density of *C. fornicata* versus various characteristics of the sediments are shown in Figure 5. Using simple linear regression, there appears to be a positive relationship between density and the percent cover of solid substrate, ash weight, and mean grain diameter, but not with percent silt or clay (Figure 5). Simple linear regression analysis, however, does not include information on interrelationships between independent variables and, thus, may not provide an accurate assessment of relationships between the dependent variable and the combination of all independent variables. Multiple regression analysis, however, does include this information and shows that 67% of the variance in density can be attributed to changes in the percent cover of solid material and that another 19% of the variance in density can be attributed to changes in the percent ash weight of the sediment (Table 2). The other independent variables do not significantly correlate with variance in density.

Characteristics of the Population

With the exception of a few stacks that had washed up alive on the beach, all of the specimens of *Crepidula fornicata* were located subtidally. The size of the stacks ranged from 1 to 11 animals with an average stack size of 3.8 animals. The substrates to which the live snails at the bottom of the stacks were attached, along with the percentage of total stacks attached to each kind of substrate, are shown in Table 3. Almost half of the stacks were attached to dead *C. fornicata* shells while another 34% of the stacks were attached to dead *Littorina littorea* shells.

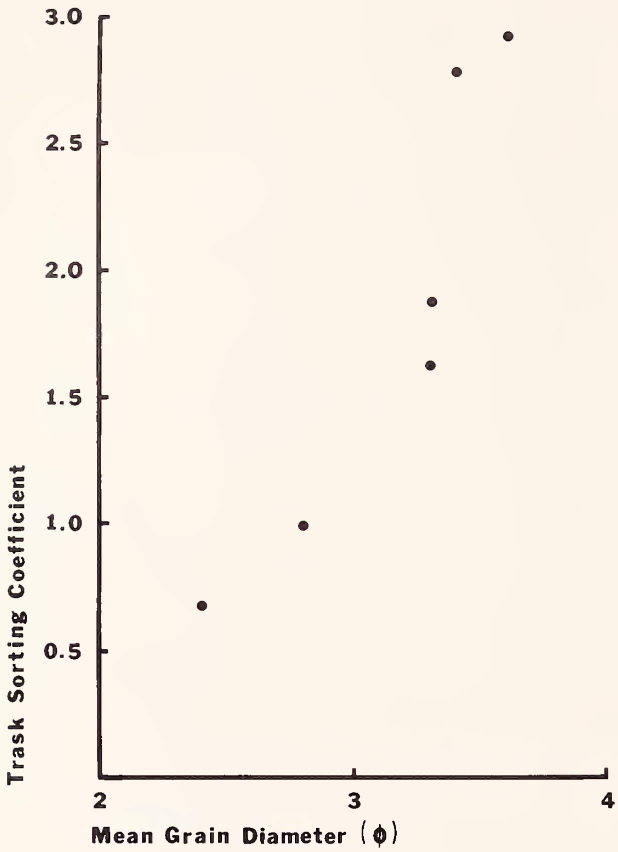

Figure 4

The relationship between mean grain diameter and the sorting of the sediments from the study site.

The rest of the stacks were attached to the shells of various dead mollusks, dead horseshoe crabs (*Limulus*), or glass bottles. All of the *C. fornicata* stacks except those attached to dead *Limulus* or bottles were lying on their right or left side and that side was buried at least 1 cm deep in the substratum with the other side exposed to water. The density of *C. fornicata* ranged from 0 to 43 individuals/m^2. The percent cover of solid substrate (shells, wood, and bottles), which may be a measurement of the amount of space available for the recruitment of new individuals (HOAGLAND, 1979), ranged from 0 where there were no *C. fornicata* to 9.4 where the density of snails was highest.

Behavioral Observations

Initial observations of the movement of water currents into and out of the mantle cavity of *Crepidula fornicata* indicated that postural changes of the snails might be important in feeding when the animals are associated with soft substrates. As *C. fornicata* rests upon the shell below it, an opening is produced at the anterior end where the animal's shell margin meets the lower shell. The snails appeared to undergo a cycle of movements that involved changing the width of this opening. These movements were measured using a physiograph and the results from one animal are presented in Figure 6. The cycle begins when the snail rapidly closes the aperture. This movement results in the rapid expulsion of water from the mantle cavity which resuspends sediments into the water adjacent to the animal. The aperture remains closed for a short period of time and then opens again. When the aperture is opened, water rushes into the mantle cavity. The aperture remains open while the snail filters the resuspended sediments from the water. Small movements while the aperture is open may facilitate the movement of water into and out of the mantle cavity. The cycle begins again with the rapid closure of the aperture. The postural movements have the secondary effect of clearing a free space in the sediment just below the anterior end of the animals so that water can circulate freely whether the stacks are on their right or left side. Similar results were obtained from all snails tested whether associated with sediments or not.

Table 2

Stepwise multiple regression analysis of density of *Crepidula fornicata vs.* percent cover of solid substrate (COV), organic content (OC), percent silt and clay (SC), mean grain size (MGS), and depth (DEP). NS represents no significant information added.

Variable	r^2	Change in r^2	Significance
COV	0.669	0.669	$P < 0.001$
OC	0.863	0.194	$P < 0.05$
SC	0.870	0.007	NS
DEP	0.905	0.036	NS
MGS	0.924	0.019	NS

DISCUSSION

Crepidula fornicata in the Pataguanset River is associated with sediments that have a silt and clay content ranging

Table 3

Substrates to which *Crepidula fornicata* stacks were attached.

Substrate	Number of stacks	% of total stacks
Crepidula fornicata	52	44.8
Littorina littorea	39	33.6
Bottle	7	6.0
Mytilus edulis	6	5.2
Mercenaria mercenaria	6	5.2
Limulus polyphemus	5	4.3
Busycon canaliculatum	1	0.9

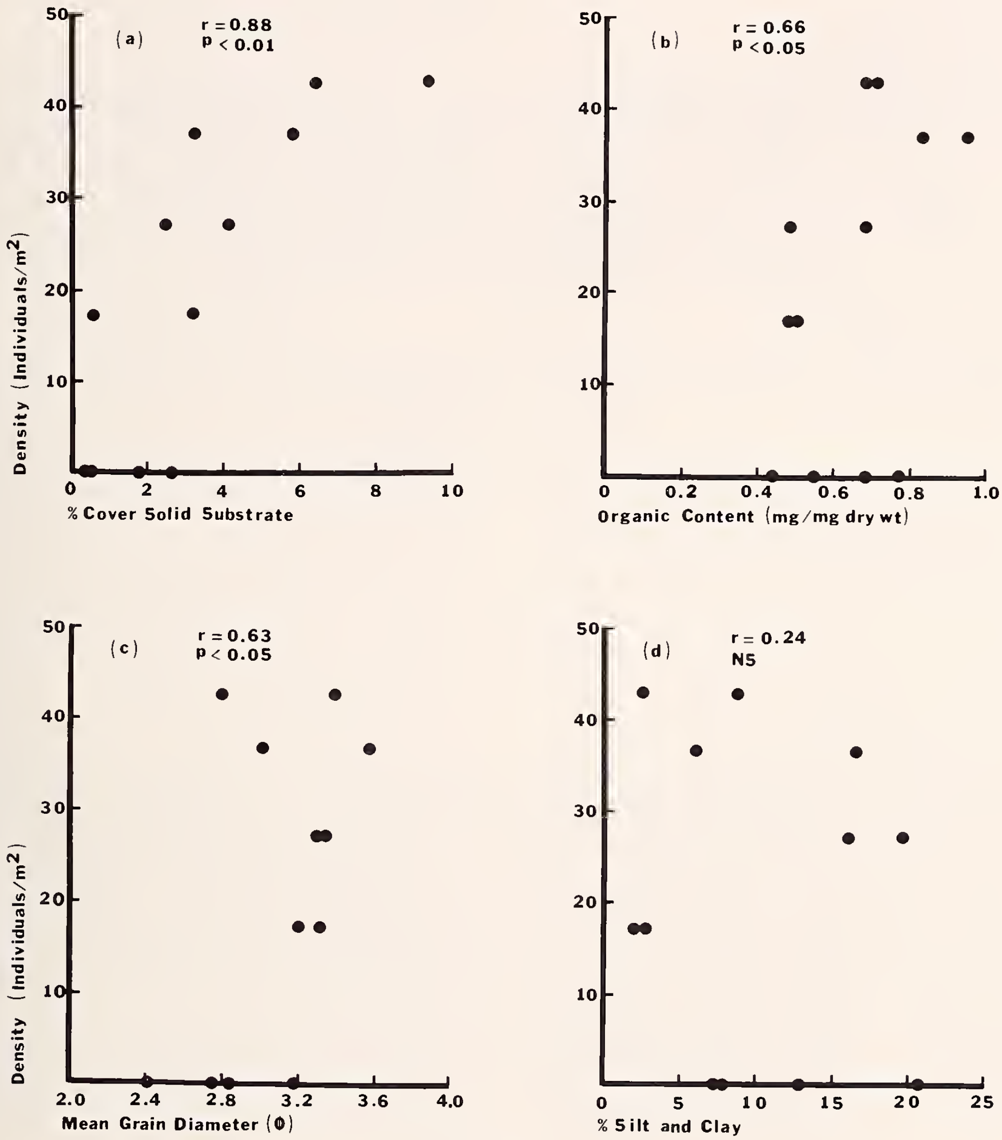

Figure 5

Scattergrams of the density of *Crepidula fornicata vs.* percent cover solid substrate (a), organic content of the sediments (b), mean grain diameter of the sediments (c), and percent silt and clay in the sediments (d) (*r* value and significance factors are given for linear regression of each of the independent variables).

from 0.2 to 19.6%, a mean grain diameter ranging from 3.6 ϕ (0.08 mm) to 2.4 ϕ (0.185 mm), organic content ranging from 0.44 to 1.79%, and cover of solid substrate ranging from 0.5 to 10%. The only sediment characteristics that were correlated with the density of *C. fornicata* were percent cover of solid substrate and organic content.

The correlation between cover of solid substrate and the density of *Crepidula fornicata* is not surprising considering that the larvae of the snails require a solid substrate upon which to settle (Hoagland, 1979). A new population would not become established in areas that had no solid substrate, and the greater the cover of solid substrate, the greater would be the chances for the establishment of new stacks. Driscoll (1967) obtained similar results in a study of attached epifauna-substrate relations in Buzzards Bay, Massachusetts. He found that the highest densities of *C. fornicata* were associated with "shell-rich" substrates, although he did not present quantitative data on the amount of solid substrate present.

The correlation between the organic content of the sed-

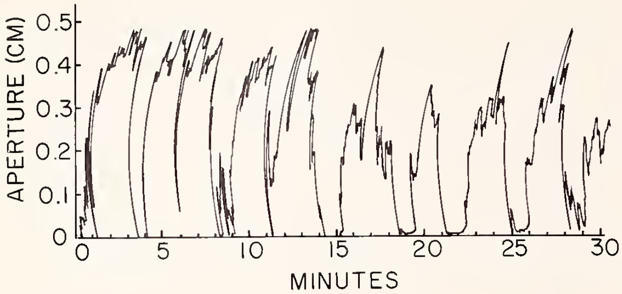

Figure 6

Physiograph recording of postural movements of an individual *Crepidula fornicata*.

iments and the density of *Crepidula fornicata* is not as easily explained. Most epifaunal suspension feeders are associated with sediments that have a low silt and clay content and a mean grain diameter in the medium sand range (SANDERS, 1958; DRISCOLL, 1967). This study and others (DRISCOLL, 1967; DRISCOLL & BRANDON, 1973; BARNES *et al.*, 1973) suggest that *C. fornicata* is anomalous in that it is an epifaunal suspension feeder but it is associated with finer grained sediments that have a high silt and clay content, high organic content, and whose sorting becomes increasingly poor with decreasing mean grain diameter. One reason that epifaunal suspension feeders are not associated with finer grained sediments may be low food availability in the water above these sediments (TURPAEVA, 1959; SANDERS, 1958; DRISCOLL, 1967). If *C. fornicata* could utilize the organic matter in the sediments as a food source, it might be able to survive on sediments that exclude other epifaunal suspension feeders. It appears that *C. fornicata* does have such a mechanism. Postural changes allow the snails to resuspend fine sediments and filter them from the water. This mechanism would require that the organic content of the sediments be high enough to satisfy the oxidative requirements of the animal. Therefore, the higher the organic content of the sediments, the more likely it is that *C. fornicata* could survive and reproduce. Another explanation for the exclusion of epifaunal suspension feeders from finer grained sediments may be that their filtering mechanism is clogged by very fine surface sediments that are resuspended by low velocity tidal flow (RHOADS & YOUNG, 1970). The efficiency of filter feeding of *Crepidula* does decrease under turbid conditions (JOHNSON, 1971), but it is likely that a higher organic content of the sediments could compensate for this decreased efficiency.

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